

Five eggs measure :  $1.87 \times 1.37$  ;  $1.87 \times 1.31$  ;  $1.81 \times 1.25$  ;  $1.81 \times 1.37$  ;  $1.75 \times 1.38$  inch.

In colour the young birds repeat the pattern of their parents. The head and occiput are clear greyish white, even lighter than the ashy head of the adult. The lores and postorbital spaces are black. The other parts are sooty black. The legs and feet are dark brown, affording no hint of the yellow or orange hue of maturity.

XX.—*On the Anatomy of the Radiated Fruit-Cuckoo* (*Carpococcyx radiatus*). By FRANK E. BEDDARD, M.A., F.R.S.

So far as I am aware, there is no published account of the anatomy of *Carpococcyx*. Being particularly interested in the group of Cuckoos, I am glad to have this opportunity of contributing to ornithology some account of its structure, which is based upon a specimen recently living in the Gardens of the Zoological Society of London\*.

a. *External Characters.*

As in Cuckoos generally, the *oil-gland* is nude.

I counted 10 rectrices and 18 remiges. The fifth cubital remex is *not* missing.

The ventral feather-tracts in *Carpococcyx* separate from each other about halfway down the neck. On the breast the tract of each side is not more than two or three feathers wide. A small tract of feeble feathers runs thence to the hypopteron. At about the middle of the sternum the tract divides, and each half is very rapidly reduced to the width of a single feather. There is no union of the divided tracts whatever at the cloaca or anywhere else ; they are completely separate throughout.

Dorsally there is a very marked break between the cervical

\* Received August 31st, 1882. See P. Z. S. 1882, p. 358. It lived nearly 18 years in the Gardens, and died June 7th, 1900. It was fed mostly on a vegetable diet with a little scraped raw meat intermixed ; occasionally insects were given, and a dead mouse every other day.

portion of the dorsal tract and the rest. The spinal tract is at first narrow, but is broader posteriorly from the level of the articulation of the femora; it terminates at the base of the oil-gland. It is connected at the sides by sparse feathering with the femoral tracts. There is no median apterion.

It is clear that the pterylosis of *Carpococcyx* conforms generally to the plan of arrangement which characterizes such Cuckoos as *Centropus*\*, for the ventral tract of each side divides upon the breast to form two separate tracts, which, as in *Centropus celebensis*, retain their individuality to the end. There is also an agreement with many Cuckoos in the fact that there is a marked break, absolutely without feathers, between the cervical and dorsal portions of the spinal tract. The principal difference which distinguishes *Carpococcyx* from all Cuckoos the pterylosis of which has been examined and recorded is the unbroken nature of the spinal tract. There was no trace that I could discover of a median apterion. So far this is diagnostic of the genus.

#### b. Abdominal Cavity.

The two liver-lobes extend down considerably beyond the sternum, and the right is larger than the left. Each of them, as in other Cuckoos†, and in some birds besides, is entirely shut off in a compartment of its own. There is no communication, that can be detected on dissection, between these chambers and that which lodges the intestine. The nature, however, of the right and left hepatic sacs is not quite the same. When the abdominal wall in the neighbourhood of the gizzard was removed, what appeared to be the falciform ligament was seen to pass from the gizzard between the two lobes of the liver to the sternum. A further dissection, however, showed that this apparently single membrane was double, a wide space between the two

\* Beddard, "On the Structural Characters and Classification of the Cuckoos," P. Z. S. 1885, p. 168.

† Beddard, "On the Anatomy of an Australian Cuckoo (*Scythrops novaehollandiae*)," P. Z. S. 1898, p. 44.

being empty of viscera, save for a portion of the gizzard, which projected into it. Of the two vertical membranes that on the left seemed to me to be the real equivalent of the falciform ligament of other birds; for it was attached to the sternum in the middle line and to the gizzard approximately so; moreover, it carried blood-vessels. The right hepatic recess has thus its own median wall, while that of the left hepatic recess is formed by the falciform ligament. I have used the expression "median" as indicating the position of that septum with regard to the two hepatic chambers. As a matter of fact, the septum in question is rather oblique in its direction, trending distinctly towards the right side of the body. It has been, I imagine, pushed backwards by the growth of the liver-lobe, and really corresponds to the transverse partition which shuts off the same liver-lobe in *Scythrops*\*.

#### c. *Alimentary Canal.*

The intestines are, as in the Cuckoos generally, short. The small intestines measure 24 inches; the large intestines only 2 inches, or a trifle more; the cæca 3 inches. It has already been mentioned that the right lobe of the liver is the larger. The gall-bladder is very large, and its duct, the hepatic duct, and the pancreatic duct open into the small intestine at the top of the **U** in the order mentioned, the first-named duct being furthest away from the pylorus.

The proportion of the length of the cæca to the length of the intestines does not differ widely from what is seen in other genera, saving only *Scythrops*, which appears to have abnormally long cæca †.

#### d. *The Windpipe.*

The syrinx of *Carpococcyx* (figs. 20, 21, p. 203) is the most purely bronchial syrinx that exists among the Cuculidæ; it is even more exaggerated than that of *Crotophaga*. To the syrinx of the latter genus that of *Carpococcyx* bears the closest

\* See Beddard, *loc. cit.*

† See Beddard, 'The Structure and Classification of Birds' (London, 1899), the table on p. 279.

resemblance. It is not, however, in my opinion, necessary on this account to place the two genera in especially close proximity, a proceeding which geographical considerations do not favour. I am inclined to believe that the peculiar form of the bronchi of these two Cuckoos may have been independently arrived at by a closing up of the rings in

Fig. 20.



Syrinx of *Carpodoccyx radiatus*  
(nat. size), anterior view.

Fig. 21.



The same, lateral view.

the upper region of the bronchi like those of the Old-World *Centropus* or of the New-World *Geococcyx*. These two genera, in fact, seem so far as their windpipes are concerned, to present us with an intermediate stage between the typical trachco-bronchial syrinx of the Phœnicophainæ and the extraordinarily specialized bronchial syrinx of *Crotophaga* and of *Carpodoccyx*.

The syrinx of the latter genus is represented in figs. 20, 21, which show anterior and lateral views of the organ. The trachea divides into the two bronchi after the fashion, as it has been remarked, of the trachea of a mammal. For the space of about an inch each bronchus consists of perfectly complete rings, of which there are 22 running right round the tube. This region of the bronchus is therefore composed of many more rings than in *Crotophaga*, which has rather less than half the number. The intrinsic muscles of the syrinx run down the bronchi and are inserted on to the third of the bronchial semirings. This ring is bowed in form, the concavity being downwards, and is, in fact, exactly like the third bronchial semiring of typically tracheo-bronchial syringes.

A wide membranous space separates this ring from the next, which, like it and the following, is cartilaginous. The closed rings of the bronchi are ossified.

With the first incomplete bronchial rings commences the *membrana tympaniformis interna*, which continues to the entrance of the bronchus into the lung. Herein the syrinx of *Carpococcyx* agrees with that of *Crotophaga*. In *Steatornis*, which represents for the Goatsuckers the most extreme development of the bronchial syrinx, the *membrana tympaniformis interna* is of more limited extent, being succeeded, as well as preceded, by complete closed rings.

#### e. *Muscular Anatomy.*

The materials for a comparison of the muscular anatomy of the fore limb in the Cuculidæ does not at present exist, since so small a number of types have been hitherto dissected. Fürbringer studied only the three genera *Phaenicophaes*, *Zanclostomus*, and *Cuculus*, including two species of the last-named genus, and no other author seems to have treated of their muscles in any detail. I hope to have an opportunity later of examining some other genera of Cuculidæ. In the meantime I attempt to supplement Prof. Fürbringer's account by the record of the following observations. They have been compared with his accounts

of his dissections, which are fully stated and easy for use in comparison.

*Latissimus dorsi*.—The *l. d. anterior*, whose area of origin from the vertebral column is just a fraction less than one-half of the diameter of the *l. d. posterior* at its origin, does not appear to me to be so completely fused with the latter as is asserted by Fürbringer to be the case in the Cuckoos dissected by him. The *l. d. anterior* slightly overlaps the *posterior*, and is only actually confluent with, and apparently indistinguishable from, the latter for the space of something like 2 mm. at the origin. Fürbringer speaks of their first becoming separate near the insertion on to the humerus.

*Latissimus dorsi metapatagialis* is a slender but obvious muscle. It is inserted in the axilla in common with the *rhomboideus superficialis*. The breadth of this muscle is about  $1\frac{1}{2}$  times that of the *profundus*. The attachment is to about  $\frac{5}{7}$  of the scapula, beginning proximally, and to that bone only.

*Rhomboideus profundus* of the present species, as in other Cuckoos, arises only from the vertebral column, and is inserted on to the distal half of the scapula.

*Propatagialis*.—The arrangement of the muscles and tendons of this system appears to be precisely that of other Cuckoos. A muscular pectoral slip ends in tendons which reinforce the long and short propatagial tendons. There is no biceps slip inserted on to the latter, and the tendon itself is simple and undivided.

The *expansor secundariorum* is present, as in other Cuckoos.

The *biceps* has, as in other Cuckoos described by Fürbringer, a single broad tendinous head, which arises from the acromion, and is "anchored" to the head of the humerus on its way down the arm.

The *anconeus* has a long slender tendon affixed to the humerus, in common with the *latissimus dorsi*.

The muscles of the fore limb do not appear, so far at least as our present knowledge goes, to afford any characters by which the numerous genera of Cuckoos can be classified.



It is quite otherwise with the hind limb, which does, in its muscular anatomy, exhibit characters of classificatory value. Garrod\* was the first to draw attention to the fact that the Cuculidæ can be divided into two series, in accordance with the presence or the absence of the accessory femoro-caudal muscle. In one series, which is represented by *Centropus*, the muscle-formula of the hind limb is ABXY +, the "full" muscle-formula; in the second series, of which the genus *Cuculus* is an example, the muscle-formula is the reduced one, AXY +. Thirteen years later† I extended this list to a number of Cuckoos not examined by Garrod, all of which proved to have either the muscle-formula ABXY + or the reduced formula AXY +.

So far as I know, there have been no further observations upon this subject.

Naturally, therefore, one of the earliest points to which I directed my attention in dissecting *Carpococcyx* was the condition of the flexor muscles of the thigh. I found that all the four muscles in question are present, well developed, and conspicuous. So that *Carpococcyx*, like *Scythrops*, *Eudynamis*, *Phænicophaes*, *Centropus*, *Geococcyx*, *Crotophaga*, and *Guira*, possesses the complete muscle-formula ABXY +.

I shall not give a full description of the attachments and insertions of these several muscles of the thigh, since they do not appear to me to present any noteworthy peculiarities.

As to other muscles, I may observe that the *gluteus maximus* has a large postacetabular extension, which completely hides the *biceps*, except just where the latter approaches the biceps sling.

Both the *peroneus longus* and the *peroneus brevis* are present.

#### f. The Skeleton.

The *skull* of *Carpococcyx* (fig. 22, p. 208) is not widely

\* "On Certain Muscles of the Thigh of Birds," &c., P. Z. S. 1873, p. 626.

† "On the Structural Characters and Classification of the Cuckoos," P. Z. S. 1885, p. 168; and "On the Anatomy of an Australian Cuckoo (*Scythrops novæ-hollandiæ*)," *ibid.* 1898, p. 44.

different from that of *Eudynamis*\*, with which I shall first of all compare it, afterwards indicating some points of likeness and unlikeness to other genera of Cuckoos. The anterior region of the skull is almost exactly the same length as the cranial, and a marked hinge-line divides the two; in *Eudynamis* the beak is relatively (as well as, of course, absolutely) shorter, and there is no hinge-line. On a dorsal view the skull of *Carpococcyx* is much less excavated in the region of the orbits, and the lacrymals do not project so much outwards; the upper surface of the skull has thus an almost regularly oval contour, more so than in any Cuckoo which I have had the opportunity of examining; the nearest approach to it is shown by *Pyrhrocentor* (fig. 24, p. 210), to which bird *Carpococcyx* is evidently closely allied.

The ventral aspect of the skull of *Carpococcyx* differs in several respects from that of *Eudynamis*. In the first place, the foramen magnum is more decidedly ventral in position, a difference which may be correlated with the ground-frequenting habits of *Carpococcyx* and the corresponding and different position of the head. I have already pointed out that *Eudynamis* has traces of basiptyergoid processes†. I did not, however, mention that, apparently in correspondence with these, the pterygoids are bowed inwards, and that each possesses a slightly projecting ridge, which may be looked upon, perhaps, as the rudiment of the pterygoid facet. In *Carpococcyx* the pterygoids are straight, and there are no traces of basiptyergoid processes.

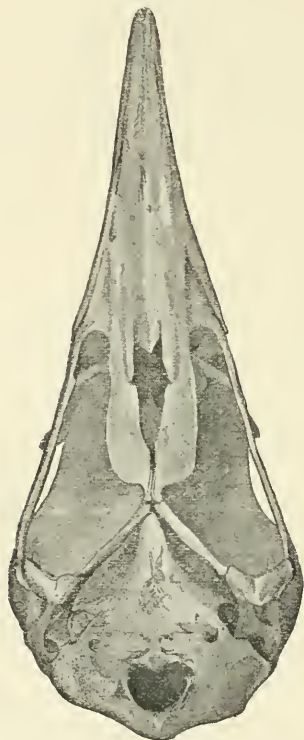
\* I select *Eudynamis* as the type of comparison, since it is, I believe, nearer to the root-stem of the Cuculidæ than any other existing genus. I mainly compare *Carpococcyx* with other genera of the Phœnicophainæ for the same reason. The skeleton of the Cuculidæ does not, indeed, appear to me to offer many facts of structure which can be used for classificatory purposes. The utmost that can be said is, I think, that the osteology of the group does not stand in contradiction to the scheme of classification which appears to me to be the right one. I cannot extract any facts which oppose themselves to, or, on the other hand, support, a division of the Cuculidæ into the three subfamilies Cuculinæ, Phœnicophainæ, and Centropodinæ.

† P. Z. S. 1898, p. 48, footnote.



The palatines are distinctly different in the two birds. In *Carpococcyx* the postero-external angles\* of the palatines are regularly and smoothly rounded off, as is shown in the accompanying figure (fig. 22). The ridges dividing the external or descending from the internal or ascending lamina

Fig. 22.



Skull of *Carpococcyx radiatus* (nat. size): ventral aspect.

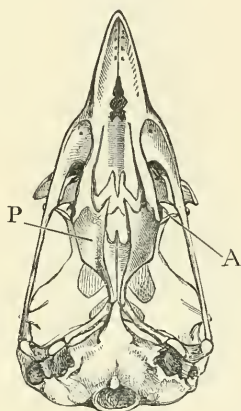
gradually approach each other, and practically come into contact for an extent occupying about the last half of the palatine symphysis. In *Eudynamis*, on the other hand, the postero-external angles (see fig. 23, p. 209) are sharply cut away, and the ventral ridges of the palatines do not come into contact anywhere, since the internal lamina of the bone is not

\* I use the nomenclature of Huxley (P. Z. S. 1867, p. 426).

aborted posteriorly, as it is in *Carpococcyx*. This difference between the two skulls is very pronounced.

The jugal arch in *Carpococcyx* passes perfectly straight to the maxilla; in *Eudynamis* it is bowed inwards at its junction with the latter bone. In neither genus are the maxillo-palatines fused for their whole extent, as they are in *Scythrops*, but *Eudynamis* shows a tendency in the direction of a more thorough desmognathism than is exhibited by *Carpococcyx*. The accompanying figure (fig. 23) shows a splint of bone running forward from the antero-internal

Fig. 23.



Skull of *Eudynamis* (nat. size), ventral aspect.

A, os uncinatum; P, palatine.

(From P. Z. S. 1898, p. 48.)

angle of the body of the palatine, which seems to foreshadow, or to be the remains of, a more massive palate, such as is possessed by *Scythrops*.

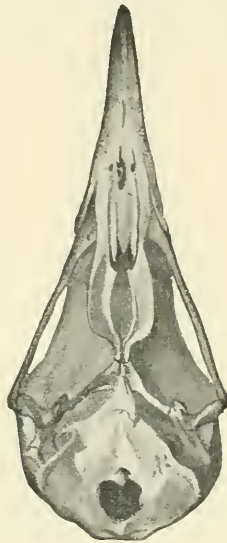
Viewed laterally, the nares of *Carpococcyx*, like those of *Eudynamis* and the majority of Cuckoos, are seen to be imperforate and single\*.

The ectethmoids are swollen rounded bones, contrasting in their appearance with the flattened ectethmoids of *Eudynamis*. The lacrymals are large, with a descending process

\* They are divided into two in *Phœnicophaes*.

that nearly reaches the jugal. The "os uncinatum" is well developed and nearly reaches the palatine. The squamosal has a much longer forwardly directed process than in *Eudynamis*, in this character approaching *Scythrops*, which does not, however, as I interpret its structure, belong to the same subfamily of Cuckoos.

Fig. 24.



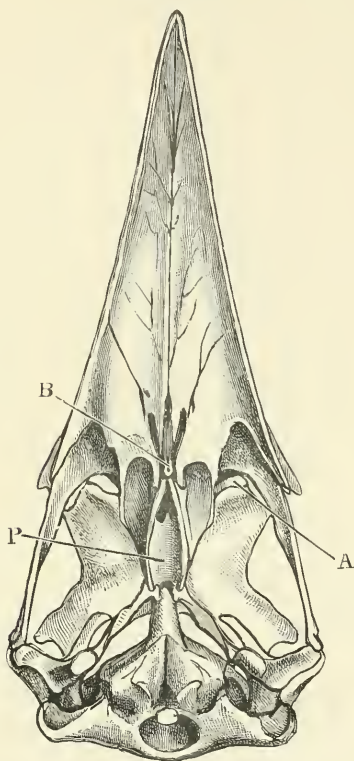
Skull of *Pyrrhocentor celebensis* (nat. size), ventral aspect.

One of the most salient points of difference which distinguishes the various genera of Cuckoos concerns the form of the palatines. *Phenicophaes* and *Rhinococcyx* (fig. 26, p. 212) (which are really hardly separable generically) stand midway structurally, if not phylogenetically, between *Carpococcyx* and *Eudynamis*; the palatine ridges come into contact for a very short space posteriorly. It may be observed also that the rudiments of basiptyergoid processes are fairly marked, but the pterygoids are not bowed inwards.

*Scythrops*, as the accompanying figure (fig. 25, p. 211) shows, has been developed from some such ground-form as *Eudynamis* in the opposite direction. In the last-named genus the palatine ridges are bent away from each other,

approaching anteriorly and posteriorly. In *Scythrops*, contrary to what we find in *Phœnicophaes*, it is the anterior regions of the ridges which come into contact. It may be

Fig. 25.

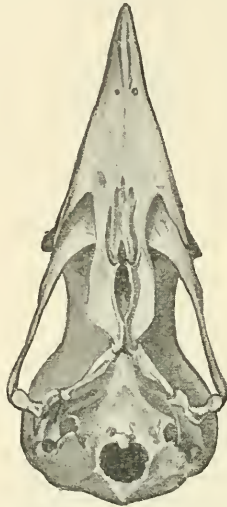
Skull of *Scythrops* (nat. size), ventral aspect.

A, os uncinatum ; P, palatines ; B, junction of palatines anteriorly.  
(From P. Z. S. 1898, p. 47.)

further remarked that the postero-external angles of the palatines in *Scythrops* are more cut away than in *Eudynamis*, while in *Phœnicophaes* and its ally the form of the angle is intermediate between that in *Eudynamis* and *Carpococcyx*. It is apparently easy, therefore, to trace the modifications of the palate through the series of genera which constitute the sub-families Phœnicophainæ and Centropodinæ in two directions.

Taking *Eudynamis* as representing most nearly the basal form not only of the subfamily Phœnicophainæ but also of the family Cuculidæ, the variations of the palate exhibited by other genera can be understood.

Fig. 26.



Skull of *Rhinococcyx curvirostris* (nat. size), ventral aspect.

In *Centropus* and *Pyrrhocentor*, representatives of the Old-World Centropodinæ, the palatine ridges are widely separated from each other, as in *Eudynamis*, and only just come in contact posteriorly, a fact most marked in *Pyrrhocentor*. *Carpococcyx* may be regarded as showing a further development of this. The same statement holds good for the New-World Centropodinæ; in short, in no other Cuckoo which I have had the opportunity of examining is there any extensive abortion of the inner lamina of the palatine posteriorly, such as exists in the Phœnicophainæ. Moreover, the considerable amount of variation in this part of the skull is distinctive of the Phœnicophainæ. This is possibly an additional argument in favour of the primitive position among the Cuckoos of that subfamily, a view which is accepted by Fürbringer.

*Vertebral column.*—There are 14 cervical vertebræ, of

which only the last two bear ribs. The atlas is perforated for the odontoid process, not notched, as in *Scythrops* and *Eudynamis*. There is no catapophysial canal formed, in which respect the genus agrees with *Scythrops* and *Eudynamis*; also, as in both these genera, the single median hypapophysis is first developed upon the 10th vertebra. Five ribs reach the sternum, there being thus one more than in *Eudynamis* and *Scythrops*. In addition, there is a tiny remnant of an eighth rib attached to the middle of the seventh, of which still more minute vestiges occur in *Scythrops*. The last dorsal vertebra, as in the two genera with which I am comparing *Carpococcyx*, is fused with the sacral series. But in *Carpococcyx*, contrary to what is found in *Eudynamis* and *Scythrops*, the last median hypapophysis is on the second dorsal vertebra; in the two last-mentioned genera it is upon the first.

The vertebral column and ribs therefore of *Carpococcyx* distinguish it from *Scythrops* and *Eudynamis*, which are naturally more nearly allied to each other.

*Sternum.*—The sternum is marked on either side by a shallow notch, as in *Scythrops*, but the bone is not so much wider posteriorly than anteriorly, as is the case with *Scythrops*. The notches are a trifle deeper than in *Scythrops*, but not so deep as in *Eudynamis*, where, however, there is, as in *Carpococcyx*, no marked widening of the sternum posteriorly.

*Hind limb.*—The proportions of the several segments of this limb naturally distinguish the ground-living *Carpococcyx* from its arboreal allies. I append a few measurements (in millim.), among which I also include those of the hind limb of the “Road-runner,” *Geococcyx*.

	Length of femur.	Length of tibia.	Length of metatarsus.
<i>Carpococcyx</i> .....	64	111	84
<i>Geococcyx</i> .....	48	66	50
<i>Scythrops</i> .....	58	77	44
<i>Eudynamis</i> .....	38	51	29
<i>Saurothera</i> .....	38	53	33
<i>Diplopterus</i> .....	29	42	32
<i>Guira</i> .....	39	60	40
<i>Piaya</i> .....	40	55	35



It will be noticed from these measurements that *Carpococcyx* has the most modified hind limb of any of the genera with which I deal. The tarso-metatarsus is relatively longer in this than in the remaining genera.

It is clear from the foregoing account of the anatomy of *Carpococcyx* that the genus is a member of that division of the family which appears to me to form a perfectly natural subfamily\*, and may be thus characterized:—

Syrinx bronchial. Ventral feather-tracts bifurcate.  
Muscle-formula ABXY +.

This family I term CENTROPODINÆ, and it has representatives both in the Old and in the New World.

The two remaining subfamilies of the Cuculidæ may be correspondingly defined thus:—

PHENICOPHAINÆ.—Syrinx tracheo-bronchial. Ventral feather-tracts bifurcate. Muscle-formula ABXY +.

CUCULINÆ.—Syrinx tracheo-bronchial. Ventral feather-tracts not bifurcate. Muscle-formula AXY +.

In conclusion, it may be useful to give a definition of the genus *Carpococcyx* for comparison with other Cuckoos:—

Genus *Carpococcyx*.—Rectrices 10; remiges 18. Eutaxial. No dorsal apterion. Each half of ventral tract ending in two separate uniserial tracts, which do not reunite. Small intestine 24 inches; cæca 3 inches. Large intestine 2 inches. Right lobe of liver > left. Gall-bladder large. Syrinx bronchial, with anterior bronchial rings complete. Muscle-formula of leg ABXY +. Cervical vertebræ 14; atlas perforated for odontoid process. Ribs  $2r + 5R + r$ . No rudiments of basipterygoid processes in skull; pterygoids straight; ridges on palatines in contact posteriorly. Nares impervious, not divided into two.

\* P. Z. S. 1885, p. 187.